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A NEW FORM OF THE TRIBE ODONASPIDINI FROM PALAWAN ISLAND, REPRESENTING A UNIQUE ADAPTIVE TYPE (STERNORRHYNCHA: COCCOIDEA: DIASPIDIDAE)

By Sadao Takagi

Abstract

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Batarasa lumampao, gen. et sp. nov., is described from the Batarasa District, Palawan Island, the Philippines. It occurs on the bamboo *Schizostachyum lumampao*, and exclusively on the node, where branches grow out. It is referable to the tribe Odonaspidini, but quite extraordinary for a member of the tribe: adult females live in a crowded colony, standing on the head; no test of distinct shape is formed; the pygidium is exposed and peculiar in structure, and is supposed to serve as a protective shield. *Batarasa* represents a unique adaptive type in association with the habitat, and thus it has established its own adaptive zone. *Batarasa lumampao* is provided with invaginated glanduliferous tubes on the pygidium in the adult female and also in the second-instar female and male. The presence of this feature may be supposed to indicate that *Batarasa* is related to *Circulaspis* and *Dicirculaspis*, but there is no further evidence for this supposed relationship.

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Contents. Introduction — Description (*Batarasa lumampao*, gen. et sp. nov.) — Relationship — Second-instar male — Niche and adaptive zone — References — Corrections — Figures.

Diaspididae or armoured scale insects have an external protection, which is called 'scale' or 'scale cover' generally and 'test' in this paper. The test is easily detachable from the insect body; in the female it is composed of the exuvial casts of the first and second nymphal instars and a cover made of secreted wax filaments and excreta (which permeate among wax filaments and probably make the test hard and, in many species, coloured); in the male it is composed of the exuvial cast of the first instar and a cover. In the very primitive species of the genus *Ulucoccus* the cover is a fluffy mass of wax filaments on the immobile body of the insect (Takagi, 1998). In the males of many Diaspidini the cover is also a loose mass on the immobile body, but in the females of most Diaspidini and the females and males of other tribes the covers are of more or less compact texture. The female tests in many species do not conform to the shape of the insect body and are obviously larger than the latter. In the males the test is completed during the second nymphal instar, whereas in the females the greater part of the test is formed in the adult stage. The construction of female tests that much exceed the size of the full-grown insect body apparently involves some movements of the body. A test that broadens backwards apparently needs pivotal and oscillatory movements, and a round test must be completed by pivotal-rotatory movements. Backward movements should be combined for constructing a still larger test, and the combination of a little of pivotal-oscillatory and much of backward movements may result in a slender long test. Matsuda (1927) made a detailed observation on the test formation in *Chrysomphalus aonidum* and depicted how the adult female rotates 'right and left or going and returning' in constructing a round test. Needless to say, the above is a rough generalization, and there are some odd tests.

Conchaspididae also construct a test that is detached from the insect body, but they are quite distinct from the Diaspididae in the structure of the body including SEM-observed details of certain features (disc pores and others) and in the SEM-observed structure of the test; the supposed complicated movements of the body in test construction are unique to them (Takagi, 1992, 1997). This supports the view that morphological evolution in Diaspididae should largely if not exclusively be associated with the manner of test construction.

The coccoid adult female is neotenic and may be regarded as an extended nymphal stage with reproductive function. In the diaspidid life cycle, as a general rule, the adult female is persistent, continuing to grow in size, constructing the greater part of the test, and breeding under the test, and thus should occupy a central position in adaptation to the sedentary juice-sucking life on the host plant. The view may be adopted that features and characters peculiar to diaspidid species have developed primarily in the stage of the adult female and are copied, with simplification or modification, into nymphs ('phenotypic attraction' in Takagi, 2008).

In spite of all this, deviation from the test-constructing mode of life has also taken place in the diaspidid evolution. The female tests of diaspidids of relatively advanced types are sometimes covered, partly or largely, with a thin upper layer of the host-plant epidermis, and this may be a preliminary step in the development of the habit of burrowing into the leaf or bark epidermis. Burrowing females may continue to form their tests, but in some cases the tests are apparently poorly formed. In *Kochummenaspis filiorum*, an extraordinary species referable to the tribe Parlatoriini, the female is naked

and free in a very broad burrow, of which the ceiling is partly lined with a thin film made of wax filaments (the second-instar exuvial cast is adhered to the wax film and the first-instar exuvial cast remains on the leaf surface) (Takagi, 2003). Gall-inducing is rare in the Diaspididae, but it is also a sideway to deviate from the diaspidid highway of evolution. According to Green (1899), the female of *Chionaspis galliformens* (now *Parachionaspis galliformens*) has no test in the gall cavity, of which the walls are lined with a thin film of wax instead (the exuvial casts are wedged in the orifice of the gall or lost); the female insect of *Chionaspis fodiens* (now *Nudachaspis fodiens*) does not construct any test, but imbeds itself in the tissues of the bark and leaves of the host plant.

Changes also occur in the body growth of the adult female. In some species, the adult female shows little or no growth in size and yet constructs a good test, apparently moving outside the exuvial cast of the second instar when constructing the test. Such species are probably exceptional, but this type of life may be precursory to the pupillarial mode of life, which is another sideway in diaspidid evolution. In the pupillarial forms, the adult female does not grow in size at all and stays under or within the exuvial cast of the second instar, and thus is no longer engaged in test construction. In many of them, the second-instar females are simplified in characters as usual in diaspidids, but in some species they are rather complicated in structure, being provided with novel features or new characters. For example, in *Annonogena*, a pupillarial genus referable to the Parlatoriini, the pygidial dorsum is modified to form the 'dorsal disc', which, when on the exuvial cast, serves as an operculum for copulation and the egress of crawlers. Moreover, the opercula in the four species of the genus are not uniform, and those in two of them bear the 'dorsal lobules', which find no analogues in other diaspidids (Takagi, 2008). It seems that in such pupillarial forms the main stage of morphological evolution has shifted from the adult female to the second-instar female, the adult being more or less reductive and modified especially in the wax-secreting organs and pygidial appendages. However, the adaptive significance of novel or new morphologies in the second-instar female is not easily understandable. The adaptive significance of the pupillarial mode itself has not been clarified, either. Actually, pupillarial forms are abundant, mostly minute and undescribed, in the tropics so far as represented in the collection at hand from tropical Asia.

The tribe Odonaspidini is a distinct group, which is well defined on the basis of the morphologies of the adult females (Ben-Dov, 1988). It is closely related to the Parlatoriini so far as based on the character pattern manifested by the second-instar males of certain species, but there is no definite trace of this relationship in the adult females of all the known species (except for the occurrence of gland tubercles on the ventral surface of the prosoma in some species). Rutherford (1915) showed this unexpected relationship for the first time (though all unawares) in describing *Parlatoria zeylanica* (p.113, not 114): this form should be the second-instar male of *Aspidiotus secretus* (now *Odonaspis secreta*), which he mentioned as one of the scale insects associated with *P. zeylanica* on the same bamboo material. (It should be kept in mind that *Odonaspis greeni*, which is very similar to *O. secreta*, was not distinguished specifically in his time.) Odonaspidini occur almost exclusively on Poaceae (Gramineae), and mainly under the leaf-sheaths, where they construct a good test. In some species the female tests are composed of flat and white dorsal and ventral portions in accord with the depressed habitat space. In others the female tests are somewhat convex dorsally, white, brownish, or blackish, and sometimes rather coriaceous, thus being similar to those of some scale insects occurring

on exposed plant parts. The nymphal exuvial casts, especially of the second-instar female, are of the bivalve type, with the dorsal and ventral portions separated for most of the body margin and connected on the head margin. This type of exuviation seems to be associated with habitation in a depressed or compressed space on the host plant, and has been observed in other tribes, too, in a few species occurring in such spaces. The bivalve type of exuviation, therefore, is not restricted to the Odonaspidini, and not all Odonaspidini belong to this type as will be shown in this paper.

The species described in this paper is associated with a bamboo (Poaceae) and occurs exclusively on the node, where branches grow out. It is referred to the tribe Odonaspidini, though it is aberrant for a member of the tribe especially in the structure of the pygidium of the adult female. No test of definite shape is formed on the female body; this fact, directly associated with the peculiar structure of the pygidium (which is almost devoid of dorsal ducts), should be a result of adaptation to the habitation on the node. Thus, this species shows another evolutionary motive factor for the disappearance of the female test.

It should be added that the male tests are formed in all the cases of deviation mentioned above (whenever the presence of the male is recognized). The test-constructing habit is not lost in those species but suppressed in the females.

DESCRIPTION

Batarasa, gen. nov.

Type species. *Batarasa lumampao*, sp. nov.

This genus is referable to the tribe Odonaspidini, subfamily Aspidiotinae. The adult female has abundant minute ducts, which are not arranged in distinct rows but strewn on both surfaces of the body, especially in paratergal and parasternal areas, and is devoid of pectinae [plates] on the pygidium and prepygidial segments. The second-instar male, nevertheless, is provided with gland tubercles on the ventral surface of the prosoma. In the first instar the antennae are five-segmented, with the third segment longer than each of the second and fourth; the tibia and tarsus in each leg are completely fused.

In the adult female the pygidium is interpreted to be composed of the fifth and succeeding abdominal segments; its dorsal surface is partitioned into a membranous anterior area, which appears to belong to the fifth abdominal segment, and a sclerotized posterior area, which is elaborately and extensively reticulate. The latter area, called 'caudal disc' hereafter, is almost devoid of ducts, and has no marginal scleroses (that mark intersegmental lines in other odonaspidines). The caudal disc is articulated with the anterior area through a strongly sclerotized transverse structure or 'hinge', which extends for most of the basal breadth of the disc. In full-grown specimens the hinge is remarkably developed; in slide-mounted specimens, it is irregularly undulate and overlaps the base of the caudal disc (in situ, the overlapping part should rise above the dermal surface), with the anterior part appearing to be inserted into the body cavity. The ventral surface of the abdomen remains membranous except for the marginal area. The marginal setae on the dorsal disc and those on the ventral side of the eighth segment are dislocated somewhat anteriorly. The anus opens on the membranous anterior area towards the base of the pygidium and thus appears to belong to the fifth abdominal segment; the vulva is placed also close to the base of the pygidium nearly at the level of the anus. Invaginated glanduliferous tubes occur on the margin of the pygidium (similar tubes also occur in the

second-instar female and male, whereas the caudal disc is peculiar to the adult female). No complete test is formed in the female; the nymphal exuvial casts are not of the bivalve type, but ruptured irregularly, remaining around the body of the female.

Only the type species is known.

Batarasa lumampao, sp. nov.

Material examined. Collected at Sitip Tig Wayan, Barangay Marrangas, Batarasa District (also spelled Bataraza), near Brooke's Point, Palawan Island, the Philippines, on *Schizostachyum lumampao* (local name: lumanpao; identified by Dr Edwino S. Fernando), 18.VIII.1993 [material no. 93PL-80]. A number of adult females, many of them being too aged and not in good condition for examination, and some specimens of the second-instar nymphs were mounted and examined.

Holotype: adult female (teneral), deposited in the collection of the Natural History Museum, University of the Philippines at Los Baños.

Habit. This species builds a colony on the node, where branches grow out. In the colony, adult females are crowded closely together, standing on the head, and their bodies grow rather plump. The exuvial casts of both nymphal instars are irregularly ruptured, with the dorsal and ventral portions often disconnected from each other, and remain around the body of the adult female. The female does not construct any distinct test; this is natural, because the caudal disc is almost devoid of ducts. The body of the full-grown adult female is partly surrounded with the exuvial casts and waxy substance secreted around, but the posterior end is naked.

The structure of the naked pygidium suggests that, in situ, the pygidium is bent towards the ventral side probably at right angles to the longitudinal axis of the body, and that the crowded colony, in which the adult females stand on the head, is roofed with their caudal discs held horizontal or nearly so. The pygidium, however, should be returned up to expose the vulva for copulation and also for oviposition or the release of crawlers (see below). (All this is no more than a speculation in the present state of study, but there seems to be no other plausible and reasonable explanation.)

This species is probably ovoviviparous, nymphs of the first instar having been observed within the bodies of some full-grown adult females.

The male constructs a slender test, with both dorsal and ventral portions formed complete. Male and female specimens were obtained from the same colonies. It seems that the male tests are formed in narrow spaces among females or around the mass of females.

Adult female (Figs 1 and 2). Teneral specimens nearly obovate or rather obpyriform, with metathorax and prepygidial abdominal segments little lobed laterally; cephalothorax and base of abdomen thickly striate in a broad marginal area with very fine wrinkle-like lines perpendicular to margin; only caudal disc and hinge strongly sclerotized. Full-grown females attaining about 1.5mm in length, often distorted in outline (probably owing to crowding in the colony); derm becoming sclerotized especially along margin of prepygidial region, but remaining membranous ventrally on abdomen to a large extent and on median area of metathorax. Antennae separated by a space as wide as frame of mouth-parts, each composed of a well-developed coronate tubercle and a curved seta. Anterior spiracles each with a group of 4–19 quinquelocular disc pores; posterior spiracles without disc pores. Ducts strewn mainly in a broad marginal-submarginal zone except on caudal disc, those on ventral surface of pygidium each opening at apex of a small membranous tubercular prominence. No perivulvar disc pores. Pygidial margin

with no distinct trullae [lobes], but provided with trulla-like prominences medially and laterally, which are not clearly demarcated and irregularly variable in shape. Reticulation on caudal disc variable in extent. An invaginated tube present on margin of segment VI, with some ducts discharging on its inner end, which is frayed to receive the ducts.

Second-instar female (Fig. 3). Having slender ducts much fewer than in adult female and scattered. Anterior spiracles each with 2–6 disc pores. Anus towards base of segment V. Pygidium with distinct median and second trullae [lobes]; median trullae set close together, broader than long, and mucronate; second trullae much smaller but distinct, followed by small conical or tubercular processes. An invaginated glanduliferous tube present between median and second trullae, with many ducts (it was not easy to count these ducts exactly; the largest number counted is 18).

Second-instar male (Figs 4 and 5). Growing elongate. Ducts in 2 sizes; broader ducts occurring in marginal-submarginal area on thoracic and basal 3 abdominal segments along posterior segmental borders, abundant on the succeeding segments except on median area. Anterior spiracles each with 3–7 disc pores. Rudiments of all legs clearly visible. Anus towards base of segment VI. Median and second trullae present, similar to those in second-instar female. An invaginated glanduliferous tube present between median and second trullae (the largest number of ducts counted is 8).

First-instar female and male (Fig. 6: exuvial cast). Sexual difference in legs inconspicuous, the male differing from the female in having only slightly shorter tibiotarsi in addition to the presence of a campaniform sensillum on each tarsus.

RELATIONSHIP

Adult females of *Batarasa lumampao* pack the narrow space of the node, standing on the head and with the pygidium exposed. This habit is unusual for an odonaspidine and even for a diaspidid and, probably in association with the habit, the pygidium is also extraordinary in structure.

Ben-Dov (1988) recognized five genera in the tribe Odonaspidini. The new genus remarkably differs from all of them in having the caudal disc, which is reticulate extensively and articulated with the membranous anterior area of the pygidium through the enormously developed hinge. As stated in the description of the species, this structure suggests a new function of the pygidium: providing the naked insect with a protective shield. *Batarasa* also differs from other odonaspidines in the anus that is not situated at the centre of the pygidium but appears to open on the fifth abdominal segment. The vulva, too, is situated close to the base of the pygidium. The shift of the anus, and also of the vulva, in position may be associated with the supposed development of the caudal disc as a protective shield.

Batarasa possesses invaginated glanduliferous tubes on the pygidial margin. This feature is present also in *Circulaspis* and *Dicirculaspis*. As understood by Ben-Dov (1988), *Circulaspis* has a single median tube, whereas *Dicirculaspis* possesses a pair of tubes laterally to the pygidial apex (between the seventh and eighth abdominal segments). These three genera, therefore, may be supposed to be closely related, but there is no further evidence for the supposed relationship.

In *Batarasa*, the invaginated tubes occur on the sixth abdominal segment in the adult female, whereas between the seventh and eighth in the second-instar female and male. This fact suggests that the position of tubes (and, therefore, also their number)

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has little generic value. Moreover, the presence or absence of this feature alone is not sufficient to separate genera (needless to say, any feature or character has no generic value by itself). When this feature is disregarded, the known odonaspidines other than *Baratasa* are rather homogeneous, and none of them seems to be especially close to *Batarasa*.

SECOND-INSTAR MALE

The second-instar males of the Diaspididae may largely be divided into two types: the 'homomorphic' second-instar males are similar to the conspecific second-instar females especially in the marginal features of the pygidium, whereas the 'heteromorphic' second-instar males are remarkably different from the second-instar females in the pygidial margin and other features. The homomorphic second-instar males differ from the conspecific second-instar females mainly in having more numerous ducts (in harmony with the fact that the male tests are completed during the second instar). Except for many pupillarial forms (in which the adult females are more or less simplified in body structure), the second-instar females are similar to the conspecific adult females in the pygidial margin, differing from the latter especially in having much fewer ducts (because, in the female, the test is constructed largely by the adult), so that, as a rule, the homomorphic second-instar males are similar also to the conspecific adult females in the pygidial margin and, as compared with the second-instar females, in having abundant ducts.

Sometimes homo- and heteromorphic second-instar males occur within a group of species that are closely similar in the adult females and, therefore, probably closely related. In such a group the males of both types should not be much different behaviourally, and it is doubted if the remarkable morphological difference between the homo- and heteromorphic forms has any adaptive significance in their life. The view may be adopted that the phenotypic pattern in the second-instar male is suddenly and drastically alterable incidentally to a slight change in the genome caused by the evolving adult female. The homomorphic males are apparently 'attracted' to the conspecific adult females in their phenotypes, whereas the heteromorphic males may represent morphological patterns that otherwise are latent as 'prepatterns' (Sondhi, 1962) or 'blueprints' in the genomes of the species. In many species of the Diaspidini the heteromorphic males are similar to the adult females of the very primitive genus *Ulucoccus*. In some species of the Odonaspidini the heteromorphic males exhibit a pattern that is obviously common to the distinct tribe Parlatoriini; this phenomenon may be titled 'Parlatoriini amongst the Odonaspidini' in emulation of the marvellous essay 'A breadfruit amongst the dipterocarps: galls and atavism' (Jenkins and Mabberley, 1994), and likewise suggests the atavistic nature of the heteromorphic forms. *Smilacicola*, the tribe Smilacicolini, has parlatoriine-patterned nymphs not only in the male but also in the female. All these odd forms should reflect ancestral adult female phenotypes, which are manifested naturally with some modifications in the second-instar nymphs.

In reality, however, the simple dichotomy into the homo- and heteromorphic types is not always adequate to describe forms in the diaspidid second-instar male. Our knowledge of this stage is still fragmentary, but there seems to be a spectrum of forms between the discrete types, which represent its extremes. Such a broad phenotypic variation involving atavism and sometimes exhibited by closely related species

necessarily requires an insight into the genetic system behind it. As has been postulated by some authors, the genetic background for phenotypic evolution should be build up with 'gene batteries', each of which is composed of elements hierarchically 'wired' in function; they should be organized to form intricate networks and yet dissociable to various degrees and thus capable of overlapping in various ways (an early model: Britten and Davidson, 1969). Overlapping batteries of genes are comparable to interconnected electric circuits with many switches, and 'the potential outputs of switches are virtually endless', though 'the actual set of switches in any animal is finite' (Carroll, 2005). In the diaspidid second-instar males, a set of activated circuits or batteries will lead to a homomorphic phenotype, whereas another set, probably partly or largely concurring with the former and activated by a change in the genome caused by the evolving adult female, may retrace an ancestral network of wiring, a 'blueprint' in the genome, thus recalling an ancestral pattern of gene expression and producing an atavistic phenotype, which is heteromorphic. Other changes in switching, caused likewise by the evolving adult females, may result in forms variegated between the homo- and heteromorphic types.

In the Odonaspidini, the second-instar males of only a few species have been described or illustrated, representing the discrete types. In this stage, *Odonaspis minima* is homomorphic (Howell and Tippins, 1978), whereas *Odonaspis penicillata*, *O. secreta*, and *O. arcusnotata* are heteromorphic and patterned as in the Parlatoriini (Takagi, 1969, 1990, 2002). Furthermore, *Parlatoria zeylanica* described by Rutherford (1915: p. 113) should represent the second-instar male of *Odonaspis secreta* or *O. greeni* (see under Introduction). Actually, however, there exist variegated forms between these discrete types. (Information is now available on sexual dimorphism in the second-instar nymphs of 14 odonaspidine species: Aono, M., Taxonomic study on Odonaspidini, with particular reference to sexual dimorphism in the second instar, published on this issue of the journal.)

The second-instar male of *Batarasa lumampao* is homomorphic, being closely similar to the second-instar female especially in the marginal features of the pygidium, on which the median and second trullae are clearly recognizable and rather characteristically shaped. Contrary to the general rule, these second-instar nymphs bear no close resemblance to the adult female, which is too peculiarly modified on the pygidium. Trulla-like prominences are present in the adult female, but they are poorly demarcated from the pygidial margin and irregularly variable in shape, so that they appear to be mere undulations of the pygidial margin. In this species the adult female is much specialized, whereas the second-instar nymphs seem to be relatively conservative, and may give some idea about the state of the adult female in an unspecialized ancestral form. If this supposition is correct, the second-instar nymphs are helpful in looking for close relatives of *Batarasa*.

NICHE AND ADAPTIVE ZONE

Aonidiella aurantii and *A. citrina*, polyphagous scale insects probably native to Asia, invaded southern California in the later nineteenth century and became serious pests in citrus orchards. The two species were found on citrus trees for more than half a century, but during this period *A. aurantii* gradually replaced *A. citrina*, and the latter disappeared from citrus trees by about 1965. On citrus leaves *A. aurantii* and *A. citrina* are ecological homologues, sharing the same niche, but in southern California they co-

existed in many citrus areas for decades before the latter became extinct on citrus trees in all these areas (DeBach et al., 1978).

It is not rare to find scale insects of more than one species on the same individuals of plants and, further, on the same leaves or branches. The co-existence of closely related or similar species necessarily arouses questions: are they different or not different in their ecological requirements and, if not different, how do they co-exist? If competitive displacement in scale insects generally proceeds so slowly as shown by *Aonidiella aurantii* and *A. citrina* occurring on citrus leaves in southern California, it is impossible to draw any definite conclusion from single or short-period observations.

On the bamboo material from which *Batarasa lumampao* was obtained, two other species of the Odonaspidini and *Natalaspis formosana* were found on the branches under the leaf-sheaths. *N. formosana* was originally described in *Odonaspis* and later placed among Rugaspidiotini (which are unrelated forms assembled to form an artificial group), but it is referable to the tribe Diaspidini (Takagi, 1995). *Natalaspis* and Odonaspidini, belonging to the Diaspidinae and the Aspidiotinae, respectively, represent a remarkable example of convergence in association with their habit to live on bamboo branches under leaf-sheaths. The collection at hand from Malaysia and the Philippines shows that odonaspidines of different species occur on the same clumps of bamboo and even on the same branches not infrequently, and also that the odonaspidine-*Natalaspis* co-existence is not unusual. Rutherford (1915) recorded the co-existence of *Aspidiotus secretus* (now *Odonaspis secreta*) and *Chionaspis simplex* (now *Natalaspis simplex*) on the same bamboo material in Sri Lanka. It seems that these scale insects are very close if not the same in their ecological requirements, whereas *Batarasa lumampao* appears to be definitely different from them, occurring exclusively on the node.

The concept of adaptive zone will show the difference more clearly. This term has been used the same as ecological niche by some authors, but in its original meaning (Simpson, 1944, 1953) an adaptive zone is a niche-organism system, in which the organism represents an adaptive type corresponding to the niche (for a recent discussion, see Brock, 2000). Diaspididae have created an adaptive zone by developing a protective test of a particular structure for their sessile juice-sucking life on plants; they have exploited and broadened the zone by improving the test and modifying morphological characters of the body accordingly. The diaspidid adaptive zone has developed mainly on exposed plant parts, whereas the Odonaspidini, *Natalaspis*, and other forms have expanded it onto some hidden parts. The Odonaspidini and *Natalaspis* have modified their characters especially of the pygidial margin and wax-secreting ducts but, except for *Batarasa*, they keep on constructing their tests.

Batarasa has preferred the node, which is a narrow space but probably provides a unique micro-environment. In adaptation to this environment, test construction is suppressed in the female, and the pygidium of the adult female has been modified to a peculiar structure, which finds no analogue in the other Diaspididae. *Batarasa* represents a unique adaptive type, and thus has established its own adaptive zone. It is, nevertheless, a good diaspidid in the general body structure and, in this respect, the *Batarasa* adaptive zone is subsidiary to the grand adaptive zone of the Diaspididae and undoubtedly very narrow. In its occurrence on the node, *Batarasa* may be comparable with some species of *Antonina*, Pseudococcidae. The latter species, however, are not particularly specialized morphologically among the members of *Antonina*, which represent an adaptive type of mealybugs occurring on the node and under the leaf-sheath on bamboos and other

Poaceae. In contrast with these node-inhabiting coccoids, most Odonaspidini and *Natalaspis* live in another adaptive zone, from which *Batarasa* has escaped.

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Takagi, S., 2002 above:
p. 57, line 9 from bottom, for 'THREE' read 'TWO';
p. 71, line 2 from top, for 'angiospermes' read 'angiosperms'.

Takagi, S., 2008, above:
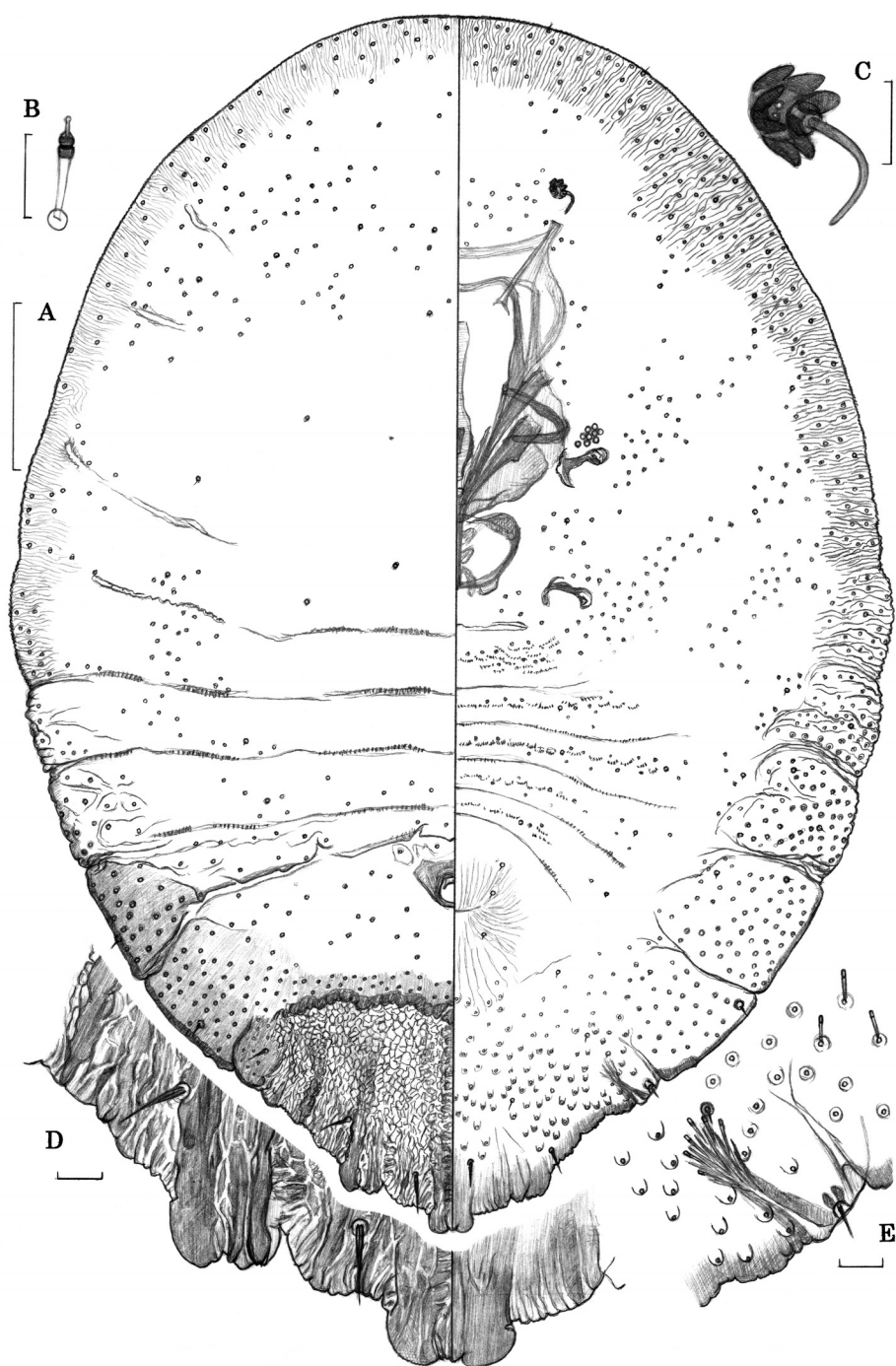p. 108, explanation for Fig. 12, for 'operculi' read 'opercula'.

Fig. 1. *Batarasa lumampao*, adult female (teneral). B, dorsal duct on prosoma; C, antenna; D, pygidial margin; E, invaginated glanduliferous tube on sixth abdominal segment. Scale bars: A, 100μm; B–E, 10μm.
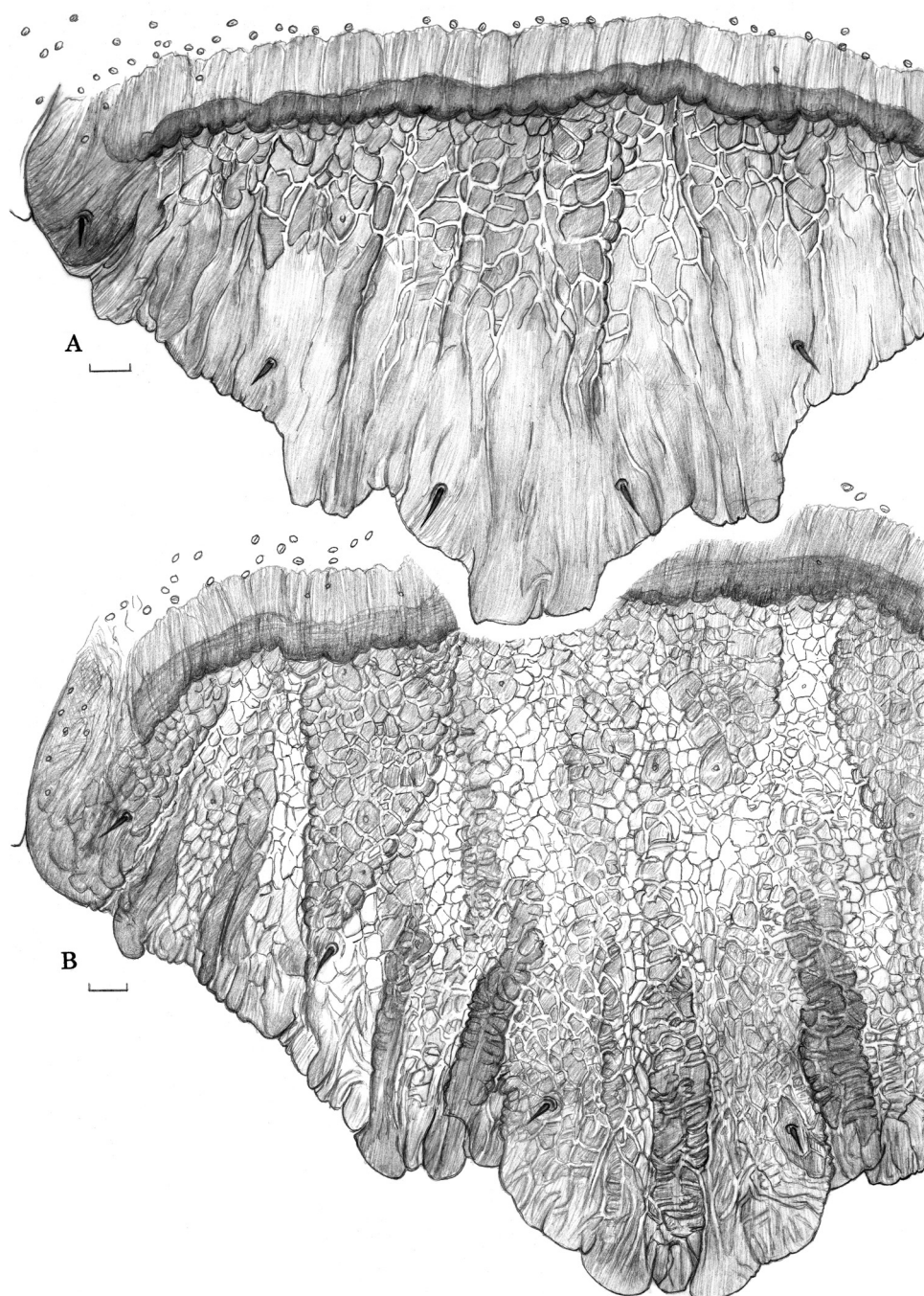
Fig. 2. *Batarasa lumampao*, adult female (full-grown), two examples of caudal disc. Scale bars: 10µm.

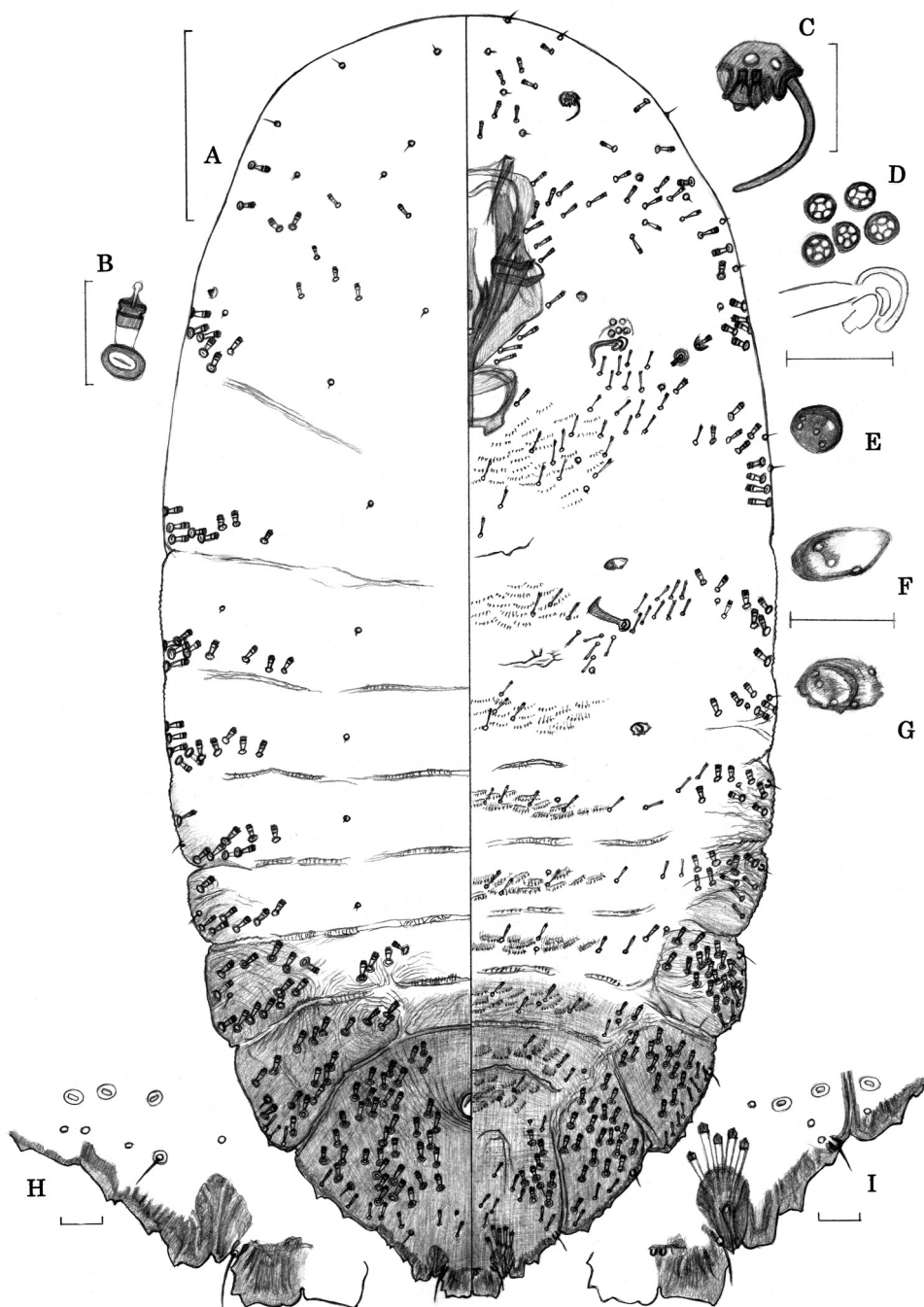Fig. 3. *Batarasa lumampao*, second-instar female. B, antenna; C, pygidial margin. Scale bars: A, 100µm; B, C, 10µm.

Fig. 4. *Batarasa lumampao*, second-instar male (nearly full-grown). B, dorsal duct on prosoma; C, antenna; D, disc pores associated with anterior spiracle; E–G, rudiments of pro-, meso-, and metathoracic legs; H, pygidial margin, dorsal; I, pygidial margin, ventral. Scale bars: A, 100µm; B–I, 10µm.
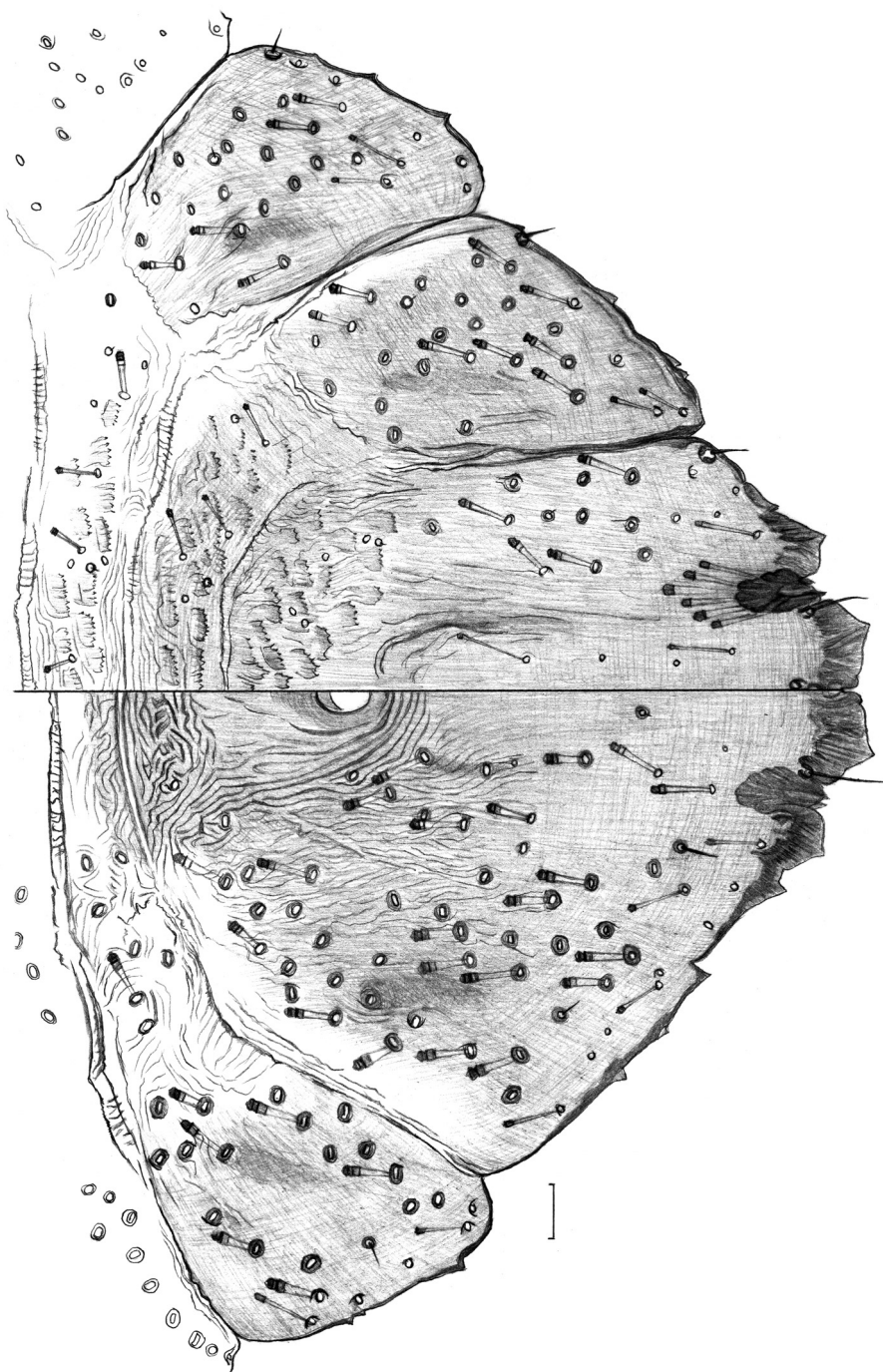
Fig. 5. *Batarasa lumampao*, second-instar male (teneral), pygidium. Scale bar: 10μm.
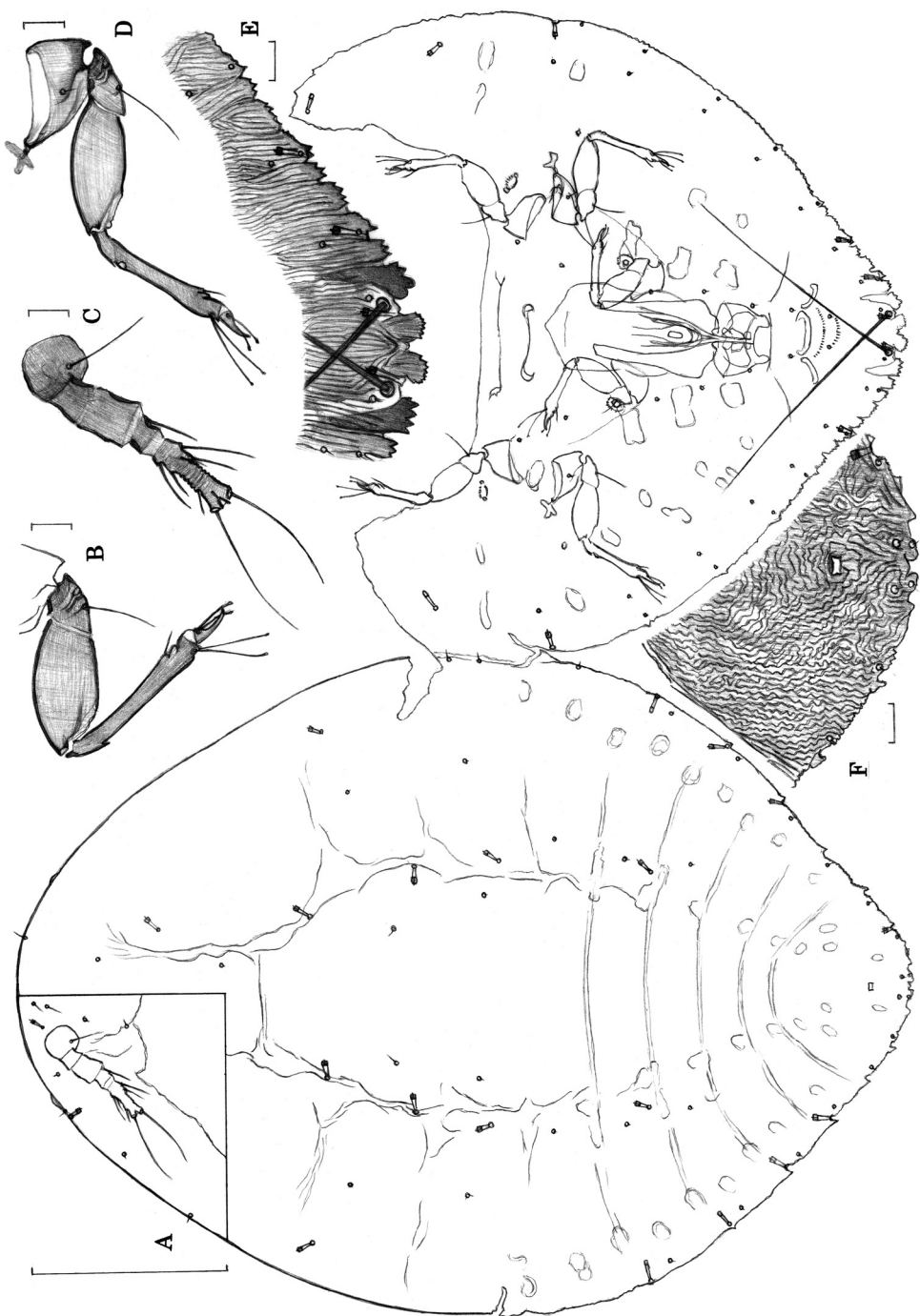
Fig. 6. *Batarasa lumampao*, first-instar exuvial cast. A, C–F, male; B, female. B, D, mesothoracic leg; C, antenna; E, pygidial margin, ventral; F, dorsal surface of pygidium. Scale bars: A, 100μm; B–F, 10μm.